Catalogue of American Amphibians and Reptiles.

UZZELL, THOMAS. 1967. *Ambystoma tremblayi.*

Ambystoma tremblayi Comeau
Tremblay's salamander

Ambystoma tremblayi Comeau, 1943: 124. Type-locality not given in original description. Brame (1959:20) stated that Comeau wrote to him that the holotype was collected at "Cap Rouge, [Quebec County], province of Quebec, Canada." Holotype apparently lost. Collector Noël-M. Comeau. Date of collection unknown.

• CONTENT. No subspecies are recognized.

• DEFINITION AND DIAGNOSIS. A triploid species ($3n = 42$) of the *Ambystoma jeffersonianum* complex that probably consists exclusively of females. These females, as members of the *A. jeffersonianum* complex, require an axillary clasp in courtship. Individuals of *A. tremblayi* are generally similar to females of *A. laterale.* The digits are moderately long. The plicae of the tongue radiate from the posterior margin of the tongue. The maxillary and premaxillary teeth are in a single row, and are bifid but not hooked. The vomerine teeth are in a single row posterior to the internal nares, usually in three groups, separated by breaks behind the nares.

The dorsum of adults is dark gray to gray-black; the venter is lighter. There are numerous bluish-white markings, especially along the lower sides; these are more diffuse than in *Ambystoma laterale.* The area around the vent is black. Adults are 56 to 94 mm snout to vent, 93 to 160 mm total, with 3.3 to 4.7 mm between the external nares. The enlarged ovarian eggs number 61 to 287.

• DESCRIPTIONS. Eggs, egg masses and deposition sites were briefly described by Clanton (1934) and Uzzell (1964). The eggs are laid in small bunches (fewer singles than in *A. laterale*) on the bottom of ponds or are attached to submerged sticks; the masses have more eggs and slightly larger outer envelopes (7 to 10 mm in diameter; unpublished). The freshly dissected ovarian eggs average larger in diameter (1. 81 to 2.23 mm, mean 2.1) than eggs of *A. laterale* (Clanton, 1934).

Larvae and juveniles have not been described. Adults were described by Clanton (1934), Comeau (1943), and Uzzell (1964); hybrids between *A. laterale* and *A. jeffersonianum* described by Minton (1954) are mainly this species.

• ILLUSTRATIONS. Illustrations were published by Clanton (1934) and Uzzell (1964); Minton's (1954) photograph of a presumed hybrid between *A. laterale* and *A. jeffersonianum* probably represents this species. Eggs, egg masses, larvae, and juveniles have not been illustrated.

• DISTRIBUTION. This species is associated with the similar *Ambystoma laterale* at localities north of the Wisconsin glacial border from northern Indiana and southern Michigan east through southern Quebec to the coastal plain of Massachusetts; there is a single record for northwestern Wisconsin. All localities are within the eastern deciduous forest formation.

• FOSSIL RECORD. None.

• PERTINENT LITERATURE. Few papers deal explicitly with this species, although many referring to *A. jeffersonianum* were probably based in part on *A. tremblayi* (see REMARKS). Brame (1959) discussed the validity of the name *tremblayi.* Clanton (1934) recognized these as a distinct group of females and described morphological features distinguishing them from *A. laterale*; he also noted the sex ratio of the progeny, poor success of eggs laid, and sex ratios of mixed populations of this species and *A. laterale.* Uzzell (1963) noted the triploidy of this species. Macgregor & Uzzell (1964) described the meiotic mechanism. Uzzell (1964) described morphology, distinctions from other members of the *A. jeffersonianum* complex (*A. jeffersonianum, A. platineum, A. laterale*), sex of progeny, and cell size. Uzzell & Goldblatt (1967) discussed certain serum proteins, the hybrid origin of this species, and the role of mating preference in the distribution of this species. Other references are cited in the remainder of the text.

• REMARKS. Erythrocytes and erythrocyte nuclei probably have about 1.5 times the volume of erythrocytes and erythrocyte nuclei of the two diploid species, *A. laterale* and *A. jeffersonianum* (Uzzell, 1964), and approximate the volume of those of *A. platineum.* Ova of this species have about twice the volume of ova of *A. laterale* (Uzzell, 1964).

Epidermal cells of larvae of this species have $3n = 42$ chromosomes (Uzzell, 1963). In early diplotene of the first meiotic division, the lampbrush chromosomes of the oocytes have about twice the number of chiasmata per bivalent for each bivalent as the corresponding bivalents of *A. laterale.* Erythrocyte nuclei of adults have 1.5 times as much DNA as nuclei of *A. laterale* (Macgregor & Uzzell, 1964). The nucleoli of oocytes average about 3700, about 3 times as many as are found in *A. laterale* (Macgregor, 1965).

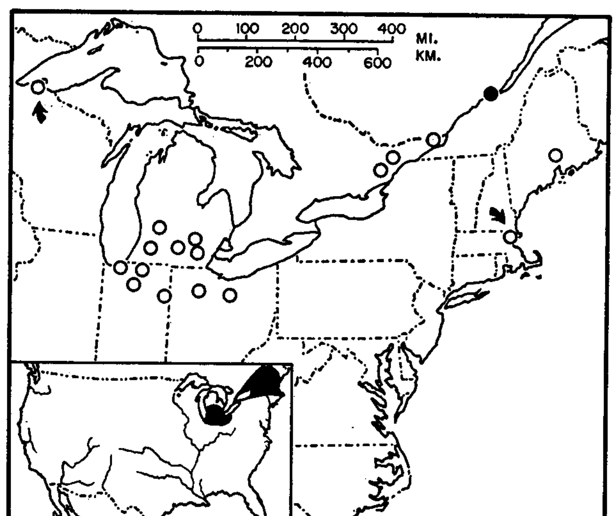
This species produces exclusively female progeny (Clanton, 1934; Uzzell, 1964).

Females of *A. tremblayi* confined with males of *A. laterale* deposited eggs that developed if the male with them produced spermatophores; when the males did not deposit spermatophores, the eggs of *A. tremblayi,* if spawned, did not develop; activation of the ova by sperm entry appears to be necessary to development (Uzzell, 1964).

Males of *Ambystoma laterale* produce small numbers of spermatophores each breeding season (Clanton, 1934; Uzzell, 1964); where females of *Ambystoma tremblayi* are greatly in excess of the males of *A. laterale,* many of their eggs probably do not get activated.

Sex ratios in mixed populations of this species and *Ambystoma laterale* near Ann Arbor, Michigan, are often highly unbalanced (Clanton, 1934; Uzzell, 1964). The highly unbalanced sex ratios reported near Toronto, York County, Ontario, by Smith (1911) and near South Bend, St. Joseph County, Indiana, by Peckham & Dineen (1955) possibly are based on this species, but may be based on *A. platineum.* Associated with the highly unbalanced sex ratio at Toronto was a very low percentage of egg development, partly due to polyspermy, but mainly associated with failure of the eggs to cleave, probably due to absence of sperm penetration (Piersol, 1929). Similar low percentages of development are associated with highly unbalanced sex ratios in mixed populations of *A. tremblayi* and *A. laterale* near Ann Arbor (Clanton, 1934).

The meiotic mechanism by which this triploid species maintains itself involves a mitotic chromosomal duplication without cytokinesis prior to meiosis; meiosis produces triploid ova; activation by sperm occurs, but syngamy apparently does not (Macgregor & Uzzell, 1964). The premeiotic duplication of chromosomes without cytokinesis and the subsequent formation of bivalents from the daughter chromosomes of this division probably vitiate the effects of crossing over and random assortment, producing genetically identical ova (Mac-



MAP. The solid circle marks the type-locality. Hollow symbols indicate other localities, the most widely disjunct indicated by arrows.

gregor & Uzzell, 1964); it may also account for the reduced fecundity of *A. tremblayi* compared to *A. laterale* (Uzzell & Goldblatt, 1967).

That *Ambystoma tremblayi* (see also *A. platineum*) is intermediate in color, relative snout width, and size between females of *A. laterale* and *A. jeffersonianum* suggests that *A. tremblayi* arose by hybridization of *A. laterale* and *A. jeffersonianum*. The localization of *A. tremblayi* (see also *A. platineum*) in those areas in which the ranges of *A. jeffersonianum* and *A. laterale* are close together also suggests hybrid origin of the triploid species (Uzzell, 1964). A serum protein characteristic of *A. laterale* (electrophoretic mobility 0.77 relative to the mobility of bovine serum albumin) and another characteristic of *A. jeffersonianum* (relative mobility 0.67) both occur in *A. tremblayi*; the relative quantities of these proteins suggest that *A. tremblayi* has two sets of *A. laterale* chromosomes, and one set of *A. jeffersonianum* chromosomes; this interpretation is consistent with the morphological and geographical data (Uzzell & Goldblatt, 1967).

Mating preference has been tested by confining, as bisexual pairs, various combinations of the two kinds of males and four kinds of females of the *Ambystoma jeffersonianum* complex in breeding cages; measured by frequency of deposition of eggs that develop, *A. tremblayi* is closely tied in mating preference to *A. laterale*. This biological association is probably reflected in the geographical association of the two species (Uzzell & Goldblatt, 1967).

The distribution of the four species of the *Ambystoma jeffersonianum* complex suggests that the hybridization between *Ambystoma laterale* and *A. jeffersonianum* that produced *A. tremblayi* probably occurred in early post-Wisconsin times (Uzzell, 1964).

The defense display reported by Rand (1954), undulation of the elevated tail, was probably observed in this species; the species shows this behavior, as do all species of the complex.

• Etymology. This species is dedicated to Jean-Louis Tremblay, director of the Biology Section, Université Laval, Quebec, Canada.

Comment

The name *tremblayi* is used for this species (Uzzell, 1964) because the holotype was a female with body length (total: 135 mm, tail: 60 mm) greater than any living female of *Ambystoma laterale* examined (51 to 73 mm snout to vent, 84 to 129 mm total); adult females of *A. tremblayi* range from 56 to 95 mm snout to vent, from 93 to 160 mm total. The triploid species for which the name is used occurs in Laval County, Quebec, about 225 km to the southwest of the type-locality (National Museum of Canada No. 9564).

Brame (1959) reported that the type is no longer extant and that the type-locality is Cap Rouge, Quebec; he established that *A. tremblayi* is a member of the *A. jeffersonianum* complex, but considered the name unidentifiable.

It is possible that *Plethodon persimilis* Gray, 1859, is a senior synonym for this species.

The single individual from Wisconsin was collected on Washburn Point, just north of Washburn, Bayfield County. It is identified as *A. tremblayi* because of its cell size, sex, and relative width of snout. It had both the serum protein characteristic of *A. jeffersonianum* (relative mobility 0.67) and that characteristic of *A. laterale* (relative mobility 0.77); these two proteins were in approximately a 1:2 ratio.

Among preserved specimens that resemble *A. laterale*, males can almost certainly be assigned to *A. laterale* rather than *A. tremblayi*. Females from the range of *A. tremblayi* (see Map) can be separated in many instances by the egg number relative to body length (cf. Uzzell, 1964, Fig. 23).

Living material is more readily identified. The ploidy can be determined by means of the erythrocyte area. When suspended in isotonic saline, the erythrocytes of *A. tremblayi* are about 1.5 times as large in optical section through the two longer axes as those of *A. laterale*.

Numerous specimens identified by cell size are preserved at the University of Michigan Museum of Zoology, Ann Arbor.

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